The Chorda Tympani and Middle Ear in Reptiles, Birds, and Mammals.

By

Edwin S. Goodrich, F.R.S.,
Fellow of Merton College, Oxford.

With Plates 11, 12 and 13, and 5 Text-figures.

A GREAT deal has been written of late years about the development and homology of the columella auris of reptiles and the chain of auditory ossicles of mammals; a mass of evidence has gradually been gathered from all sides supporting the view put forward by Reichert that the stapes and the columella are derived from the dorsal end of the hyoid arch, and that the incus and malleus, derived from the mandibular arch, correspond to the quadrate and articular. In the search for evidence not only has the development of the skeletal elements been studied, but also the origin of the tympanum and tympanic cavity, and the disposition of the blood-vessels, muscles, and nerves of the middle ear. It was with the intention of comparing the exact relation of these various parts in reptiles, birds, and mammals that the present work was undertaken. Since it was begun, however, so admirable and convincing a summary of the facts in favour of Reichert's view has been given by Gaupp (17) that it would seem as if the question were finally settled and little remained to be said. Yet some doubts and obscurities still remain, especially with regard to the exact relation of the chorda tympani to the first gill-slit, tympanum, and surrounding structures; so I decided to publish this paper as a small contribution to the discussion of a most important morphological problem. The

results of these researches have mostly been given in figures of reconstructions in which I have endeavoured to represent clearly the true relation of the parts dealt with, and to enable the reader easily to compare the different forms studied. The figures are no mere diagrams, but carefully made graphic reconstructions of transverse or longitudinal sections drawn with the camera lucida. As far as possible they have been shown from corresponding points of view, in uniform style, with consistent colouring; unessential details and irregularities being omitted to avoid unnecessary complication. I am indebted to various friends for the opportunity of studying many series of sections besides my own. Dr. Versluys I have to thank for lending me a series of sections of an embryo Platydactylus, and Prof. Dendy for sections of Sphenodon; Dr. Jenkinson for the loan of series of lizard, chick, and mouse embryos (from which figs. 1, 2, 3, 13, 22–26, were drawn), and Prof. J. Hill for valuable series of Ornithorhynchus and Trichosurus embryos of various stages (figs. 5, 14–21).

The chorda tympani, a twig of the main or hyomandibular branch of the facial nerve, supplies the organs of taste near the base of the tongue and the salivary glands in the region of the lower jaw. In adult mammals it issues from the seventh nerve behind the tympanic cavity, turns forward over this cavity, and makes its way to the lower jaw, passing below the chain of ossicles. Thus the chorda tympani runs downwards anterior to the tympanum and tympanic cavity and posterior to the incus and malleus. While the importance of the chorda in determining the homology of the parts of the middle ear has become more and more apparent through the work of Gaupp (16, 17), Kingsley (25), and others, there has been considerable confusion about its development and homology. It can easily be identified in birds and reptiles where it follows much the same course as in mammals; but although in these it has the same origin and destination, it always passes over the columella, being anterior to it and the tympanum, and posterior to the quadrate and articular. Stannius first suggested that the chorda tympani is homo-

logus with the post-spiracular ramus mandibularis internus of the facial nerve in Amphibia and Pisces. Balfour (1) and Dixon (7), however, compare it to a pre-spiracular branch, being doubtless misled by the then prevailing view that the tympanum represents the closing membrane of the spiracular slit. So we find Cole (11) and Herrick (20) arguing that, in spite of its similar function and peripheral distribution, the chorda cannot be homologous with the ramus mandibularis internus, because the latter is post-spiracular in position. However, it is now known that the tympanum is not developed at the point of closure of the first gill-slit, but behind it; so that a nerve may be post-spiracular and yet pre-tympanic. Long ago Froriep (15) correctly described the chorda tympani in an embryo calf as post-spiracular in origin, and the same result was recorded by Kastschenko in the pig (23), by Emmel (13) in Microtus, and Drüner in the mouse (10), while Hoffmann (21) and Versluys (31) have shown that in lizards it develops in the same way. That the chorda tympani is really homologous with the post-spiracular ramus mandibularis internus of fish and amphibians may now be considered as established, chiefly owing to the work of Gaupp (16) and Bender (2). In his recently published monograph Bender traces this nerve through the whole vertebrate series, and his conclusion is further strengthened by the results of Strong (30), Herrick (20), and others who have shown that gustatory fibres pass up this ramus in the lower forms.

My own observations on the development of the chorda, and the various reconstructions figured on Pls. 11, 12, 13 may now be described.

Reptilia.—Lacerta is the type studied. At a stage when the spiracular gill-cleft still opens to the exterior by a small pore at the dorsal edge of the first gill-pouch (Pl. 11, fig. 3), the skeleton of the first two visceral arches becomes visible as a vaguely defined blastema extending along the mandibular bar in front of the first gill-pouch, and a similar blastema in the hyoid bar behind the gill-pouch. The latter blastema reaches up to the scarcely yet defined blastema of the auditory cap-

sule, pushing in the posterior dorsal surface of the pouch and passing inwards between the facial nerve and vena capitis lateralis above and the internal carotid below. This stage corresponds nearly to that described in Platydactylus by Versluys (31), though perhaps a little earlier. Later on, as so well shown by Versluys, the continuous hyoid blastema bends sharply to form the horizontal columellar region and · the more ventral cornual region curved backwards and downwards. For a considerable time these two regions remain connected by a band of blastema in Lacerta (Pl. 11, fig. 8), though eventually separating. The more dorsal columellar region develops into a stout cartilage rod, with a foot or stapedial base fitting into the fenestra ovalis of the auditory capsule, and an expanded extra-columella applied to that region of the body-wall which will form the middle part of the tympanum (Pl. 11, figs. 6, 8, 11 ; Pl. 13, fig. 30). On the columella[1] develops about midway an upstanding dorsal process and an anterior internal process. The former has a swollen dorsal extremity which later separates off from the columella and becomes fixed on to the parotic process of the skull (Pl. 11, fig. 8). A fine ligament remains, indicating the original cartilaginous connection of this " intercalary " with the columella. The internal process (figs. 6, 9–11, 29, 30) projects towards the quadrate, with which it becomes connected by ligament.

Meanwhile, the mandibular blastema has given rise to the quadrate and Meckel's cartilage. The quadrate articulates with the parotic process above, the intercalary being wedged in between them at this point. Extending downwards to meet the articular region of Meckel's cartilage the quadrate passes outside the facial nerve, vena capitis lateralis, and facial artery (Pl. 11, figs. 7, 9).

In the earliest stage here figured, the first or spiracular

---

[1] The term " columella " is used to denote the whole rod, stretching from tympanum to fenestra ovalis. From the point where the remainder of the hyoid arch separates off, the inner or stapedial portion runs inwards, and the outer or extra-columellar portion runs outwards.

gill-split is widely open to the exterior and the first gill-pouch is in the form of a wide, somewhat obliquely flattened outgrowth (Pl. 11, figs. 1, 2). As explained above, by the time the hyoid blastema is differentiated the slit has almost closed, but still remains open by a small pore at the upper corner of the pouch (Pl. 11, fig. 3). Now, it is well known that the ganglia of the fifth, seventh, ninth, and tenth cranial nerves receive contributions from the epiblast at the top edge of the corresponding gill-slits. These are the so-called branchial sense organs (Froriep, 15; Kastschenko, 23a). Such an epidermal thickening can be seen above the first gill-slit in Lacerta in early stages (Pl. 11, figs. 1, 3; Pl. 13, fig. 27), and later on will sink in, contributing to form the geniculate ganglion. It therefore marks a fixed point very useful in the comparison both of different stages and of different animals. In Lacerta it can be followed for some little time after the closure of the first gill-slit and the separation of the first gill-pouch from the epiblast, and is seen to correspond to the anterior dorsal, inner or medial, corner of the pouch which gives rise to the recessus medialis (fig. 6 *air.*). A careful description of the development of the tympanic cavity in Lacerta has been given by El. Cords (12), and my own observations are in agreement with hers, as shown in Pl. 11, figs. 6, 8–11; Pl. 13, figs. 29 and 30. The flattened first gill-pouch separates off from the epiblast from below upwards. At the same time the lower posterior region grows outwards and forwards, and pushing inwards the original upper part of the pouch which last opened to the exterior it expands behind the quadrate to form the adult tympanic cavity. Three outgrowths or recesses of the cavity tend to surround the columella. These are an anterior inner or medial, an anterior outer or lateral, and a posterior recess. The two first grow upwards and then backwards over the columella, having between them the dorsal process, the internal process, and the chorda tympani (figs. 6 and 29). At a later stage the lateral recess meeting and opening into the posterior recess enables the tympanic cavity to completely surround the extra-columella.

By a thinning-out of the mesenchymatous wall separating the tympanic diverticulum of the gill-pouch from the superficial epidermis the tympanic membrane is formed. The tympanum is really developed, then, not from a membrane closing the spiracular slit, but, as clearly stated by Versluys (31), by the outgrowth of the first gill-pouch posterior and somewhat ventral to the spiracle and immediately in front of the hyoid arch. This outgrowth we may call the tympanic diverticulum (see diagram A, B, and C). The whole columella, and the hyoid cornu as well, are morphologically posterior to the tympanum and tympanic cavity.

Coming now to the blood-vessels, we find that the vena capitis lateralis passes forwards outside the tenth, ninth, and seventh nerves, above the columella, and on the inner side of the fifth nerve (Pl. 11, figs. 2, 3, 9). It runs on the inner side of the process dorsalis in the space included between the quadrate and the auditory capsule (Pl. 11, fig. 9; Pl. 13, figs. 29, 30). Accompanying the vein for this part of its course is the facial or stapedial artery (figs. 3, 6, 8, 9, 30). Starting from the internal carotid, which, of course, runs above the pharynx and gill-pouches, this artery passes outwards and forwards over the columella, then upwards and forwards on the outer side of the vena capitis lateralis and below the articulation of the quadrate with the skull. Versluys (31) has shown that in Platydactylus the facial artery pierces the foot of the columella, and his suggestion that it is homologous with the stapedial artery of the mammal seems to be fully justified, since it develops like the latter from the top end of the hyoid arterial arch and has the same relations (figs. 3, 14).

The position of the seventh or facial nerve in relation to the above-mentioned structures is well shown in Pl. 11, figs. 6, 8, 9, and Pl. 13, figs. 29, 30. Passing outwards and backwards from its ganglionic masses in front of the auditory capsule, the main or hyomandibular branch of the facial is seen to run across and under the vena capitis lateralis just dorsal to the first gill-slit or pouch, and then backwards and downwards behind the spiracular slit into the hyoid bar. As

already described, a connection exists in early stages between the facial and inner dorsal region of the epiblastic ingrowth forming the opening of the first gill-slit. An epidermal proliferation here contributes to the geniculate ganglion, and immediately in front of it runs forward the incipient palatine nerve. At a stage when the spiracular slit is still widely open (figs. 1, 2), the chorda tympani is already seen to arise from the hyomandibular branch of the facial behind the opening, and to run below the opening obliquely downwards and forwards into the mandibular bar. The chorda tympani is, therefore, as described in lizards by Hoffmann (21) and Versluys (31), distinctly a post-spiracular or post-trematic nerve. It first runs near the epidermis until it passes the lower edge of the gill-slit, when it turns inwards and runs along the mandibular bar and close to the floor of the buccal cavity, to which most of its fibres are doubtless distributed.

As the spiracular slit closes from below upwards the chorda tympani keeps near its lower edge, passing at first diagonally downwards to the lower jaw across the future tympanic region (figs. 3, 27). When the first gill-slit separates off from the epidermis, and as the tympanic diverticulum enlarges, the chorda tympani becomes more and more pushed up in front of the developing tympanic membrane (diagrams A, B, and C). Finally it slips inwards, so to speak, over the tympanic cavity so as to pass over the extra-columella on the inner side of the lateral recess, but outside both the dorsal and the internal process of the columella. The chorda tympani in reptiles is, therefore, primarily post-trematic and pre-tympanic, being situated between the opening of the first gill-slit and the tympanic membrane (diagram D, p. 153) as described by Versluys in Platydactylus.

A muscle has been described by Killian (24) in reptiles extending backwards from the extra-columellar to the parotic process of the skull. He calls it the stapedial muscle, and homologises it with the muscle of the same name in the Mammalia. It is the muscle called "m. extra-columellaris" by Versluys (31) in adult Geckonidæ, and also in the embryo

Lacerta, and found by him to be derived from the facialis musculature (depressor mandibulæ). Both Versluys and Gaupp accept Killian's conclusion, but it is difficult to see how this muscle, which passes outside the facial nerve (as shown in Pl. 11, fig. 8), can be homologous with the mammalian stapedial muscle situated on the inner side of the nerve (Pl. 12, fig. 16, and Pl. 13, fig. 25).

TEXT-FIG. 1.
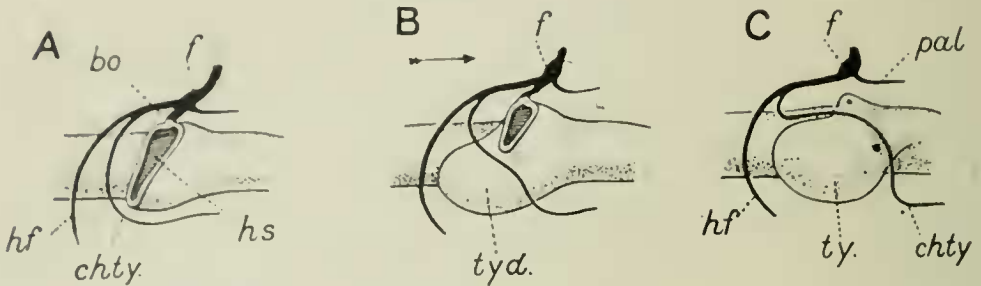
A, B. and C, Diagrams illustrating the relation of the chorda tympani nerve to the first gill-slit and the trypanum in reptiles, birds, and mammals, during ontogeny. A shows an early stage in which the slit is widely open; C, a later stage, in which the slit has closed, the gill-pouch has separated off from the epidermis, and the tympanic diverticulum has developed. B is an intermediate stage. The arrow points forwards. *bo*. Epidermal thickening ("branchial sense organ") at top of first gill-slit. *f*. Facial nerve and ganglion. *chty*. Chorda tympani. *hf*. Hyomandibular branch of facial nerve. *hs*. Hyoid or spiracular gill-slit. *pal*. Palatine nerve. *ty*. Tympanum. *tyd*. Tympanic diverticulum. (Right-side view.)

Sections of early stages of Sphenodon show that the chorda tympani develops in the same way, and bears the same relation to the first gill-slit and other structures as in Lacerta or Platydactylus. The condition described above may, therefore, be considered as typical of reptiles generally.

Aves.—So far as I am aware, the development of the chorda tympani has not yet been described in early stages of birds. Both Kastschenko (23a) and Neumayer (27) failed to find it in chick embryos less than seven and a half days old, by which time the spiracular cleft is, of course, closed and the first gill-pouch has separated from the epiblast. No

doubt these observers looked for the nerve where we should expect to find it, but where, as a matter of fact, it is not in the chick, as will be explained below.

In addition to the chick I have studied early stages in the duck, and find that this bird agrees in every essential with Lacerta. Fig. 4, Pl. 11, is a reconstruction of a four and a half-day duck embryo, where the spiracular region of the first gill-pouch is still quite continuous with the epidermis, but the skeletal blastema can hardly yet be distinguished. The vena capitis lateralis and the internal carotid bear the same relation to surrounding structures as in Lacerta. A beginning of the facial artery can be seen arising from the root of the reduced hyoid arterial arch. The outer lower region of the geniculate ganglion is attached by an epidermal proliferation, the so-called branchial sense-organ, to the dorsal part of the first gill-pouch, and the hyomandibular branch of the facial nerve passes out below the vena capitis lateralis and down into the hyoid bar (Pl. 13, fig. 28). Coming off close to the origin of the facial can be seen the chorda tympani running behind the spiracular slit, and pursuing a curved course below it into the mandibular bar, along which it can be traced near the floor of the buccal cavity. Behind the chorda tympani the first gill-pouch is growing out to form the tympanic diverticulum. Since the position of the chorda tympani in the adult duck agrees with that found in the majority of birds —Magnien (26), Bender (2), Smith (29)—we may assume that this is the normal structure and development of these parts in the Aves. The chorda tympani in every respect behaves as in Lacerta, passing over the extra-columella (extra-stapedial cartilage) and distal to the dorsal process (supra-stapedial), Smith (29).

Strangely enough, in the fowl quite another relation is borne by the chorda tympani to surrounding structures. To begin with, Hasse has shown that in the adult Gallus (19), and Magnien (26) that in the adult turkey (Meleagris gallo-pavo), this nerve takes a very unusual course. Originating quite far forwards from the geniculate ganglion, it passes

almost vertically downwards in front of the tympanic cavity to reach the articulation of the lower jaw, along which it runs as usual. Hasse and Smith both consider, I believe rightly, that this is a secondary condition; but they did not study the development, and, as already mentioned, Kastschenko and Neumayer failed to discover the chorda tympani in early stages. I have been able, however, to find it in sections of seven- and six-day chicks, and even to trace it back to the five-day chick, when the first gill-pouch is still continuous with the epiblast (Pl. 11, fig. 12). In these early stages the chorda tympani still occupies approximately the same position as in the adult bird, passing in front of the first gill-pouch from the geniculate ganglion to the mandibular bar. A minute nervous filament can be seen in the same place even in the four and a half-day chick, when the spiracle is open to the exterior.

Never at any stage have I found a chorda tympani in the chick taking the usual course behind and below the first gill-slit. Moreover, even in the earliest stages, it arises dorsally, not from the hyomandibular branch of the facial, but from the ganglionic proliferation at the dorsal edge of the spiracular slit (Pl. 11, fig. 12 ; Pl. 12, fig. 13).

It would appear, then, that in gallinaceous birds, alone among the amniote vertebrates, the chorda tympani is from its earliest appearance in the embryo a pre-trematic branch of the facial nerve. Considering how constant is the relation of nerves to surrounding structures, it is very difficult to account for this strange exception to such a general rule. The peripheral distribution of the chorda in the turkey is just like that in other birds according to Magnien (26). But perhaps the chorda tympani of the gallinaceous birds is not strictly homologous with that of other vertebrates, and it is to be noticed that it comes into relation dorsally with a complex system of slender nerves, partly sympathetic and partly palatine, which I have not followed out in detail, but have indicated in Pl. 12, fig. 13; or possibly there has been some sort of secondary short-circuiting in front of the spiracle. In any case the anomalous disposition does not appear to be due

to a mere shifting of the chorda tympani, as suggested by Smith (29), analogous to the shifting inwards of the nerve accompanying the reduction of the dorsal and internal processes of the columella found to occur in the Lacertilia, and so well described by Versluys (31). The whole question requires further investigation, and it would be interesting to know whether the chorda tympani develops in front of the first gill-slit in any other birds.

The development of the skeletal elements of the hyoid bar in the chick agrees with that described above in Lacerta. The earliest appearance of the columella has recently been studied by Smith (29), whose conclusions I can confirm. About the fifth and sixth day there is a continuous blastema representing the hyoid arch ; passing below and on the inner side of the vena capitis lateralis it merges into the blastema of the auditory capsule above. Later on the stapedial and extracolumellar regions and the various processes of the columella chondrify in this hyoid blastema. Fig. 13, Pl. 12, shows the condition in an eight-day chick : the stapedial region is in the form of a stout plug fitting into the fenestra ovalis, and continued outwards into the extra-columella. From this latter region extends downwards a long infra-stapedial or stylohyal process, almost continuous below with a small cartilage separate at this stage. The cornu of the hyoid has already become detached, and taken up a position behind the auditory region. The stylohyal and the little detached cartilage approach the posterior process of the articular cartilage of the lower jaw, and remind one of the interhyal and epihyal cartilages described by Parker in the crocodile, where they become secondarily connected with Meckel's cartilage.

This reconstruction of an eight-day chick also shows a distinct " stapedial muscle " attached to the infra-stapedial process, and occupying a position on the inner side of the hyomandibular nerve. It corresponds, therefore, to the mammalian stapedial muscle in this respect, but not to the reptilian " extra-columellar muscle."

The first gill-pouch is also seen, now, of course, detached from the epidermis. The tympanic diverticulum, however, is but little developed, the mesenchymatous tissue, into which extends the extra-columellar, between it and the ingrowing external auditory meatus, being still quite thick.

Mammalia.—As already mentioned (p. 139) the position of the chorda tympani was correctly figured and described by Froriep in early calf embryos as long ago as 1885. Broman (4), Emmel (13), and others, have since confirmed this observation, and it may now be considered as firmly established that, just as in the Reptilia so in the Mammalia, the chorda tympani arises as a post-trematic branch of the facial nerve.

My own observations fully support this conclusion. As seen in the reconstructions of early stages of Trichosurus, when the gill-pouch is still in continuity with the epidermis at a point corresponding to the open spiracular cleft of lower vertebrates, the chorda passes from the hyomandibular branch of the facial nerve round behind and below the gill-pouch to reach its destination in the mandibular arch (figs. 5 and 15). At a later stage, when the first gill-pouch is separating off from the epidermis, the chorda tympani still occupies much the same position ; and it is only later when the tympanic diverticulum develops and expands that the nerve is pushed upwards and forwards just as in Lacerta (Pl. 12, figs. 14 and 16).

Little remains to be said about the development of the auditory ossicles of the Mammalia, which has been lately so accurately described by Dreyfuss (8), Broman (4), Jenkinson (22) and others. My observations entirely support the views of these and other authors who contend that the stapes is derived from the upper end of the hyoid arch, and the incus and malleus from the upper end of the mandibular arch; as against Fuchs and others who believe otherwise (see Gaupp (17)). From the time when it first appears as a blastema in the mouse the stapes is distinct from the auditory capsule and continuous with the blastema of the remainder of the hyoid arch, passing as usual below the vena capitis

lateralis. This continuity is preserved for some time, and can still be seen quite distinctly in a 9·5 mm. Trichosurus embryo (Pl. 12, fig. 21), and a mouse (Pl. 12, fig. 22).   On the other hand, it is not continuous at these early stages with the blastema of the processus longus incudis. Soon, however, the stapes separates off from the more ventral and distal region of the hyoid arch, and chondrifies separately round the stapedial artery (figs. 22, 24). Meanwhile that region of the arch ventral to the stapes and dorsal to the future cornu, loses its connection with the stapes owing to the disappearance of the intervening zone of blastema, and then grows up round and outside the vena capitis lateralis, to become joined on to the paroccipital process of the skull (Pl. 12, figs. 16, 20 ; Pl. 13, figs. 23, 24). It is across this region of the hyoid that the chorda tympani passes on its way from the hyomandibular branch of the facial to the lower jaw (fig. 17). Named intercalare by Dreyfuss (**8**), and laterohyal by Broman (**4**), it has been aptly compared by Versluys (**31**) and Gaupp (**17**) to the intercalary cartilage developed from the dorsal process of the columella in reptiles. The two structures have the same origin, occupy the same position relative to other parts, and are probably homologous (Pl. 12, fig. 20).

In a 17 mm. Trichosurus embryo a slender cartilaginous hyoid extends continuously up to the skull (Pl. 12, fig. 16). Later on the upper region degenerates, and the more ventral part remains as the cornu of the hyoid. The developing stapes of Ornithorhynchus shows just the same relations as that of the mouse or Trichosurus, and is at first pierced by the stapedial artery.

In the mandibular bar the dorsal proximal region of the blastema differentiates as a separate cartilaginous element, the incus, and the more ventral region as Meckel's cartilage. Subsequently, as is well known, the more dorsal or articular region of this cartilage separates off as the malleus (figs. 22, 23, 24). There can now be hardly any doubt that the incus and malleus of the mammal represent the quadrate

and articular of the reptile. In the 17 mm. embryo of Trichosurus (Pl. 12, fig. 16), the incus is comparatively large and remarkably like the reptilian quadrate in its relations. Dorsally, by means of the processus brevis, it reaches up to the auditory capsule, and may be said to articulate with it, as described in the pig by Kingsley and Ruddick (**25**) ; below it articulates with the malleus. The processus longus of the incus is stout and long, and although apparently quite separate from the stapedial blastema in the earliest stages, it comes into close connection later on with the distal end of the stapes (figs. 19, 23, 25). This connection seems to me quite comparable to that established between the columella and the quadrate by means of the processus internus in reptiles, and possibly is represented by Platner's ligament in birds. In Amphibia also the stapes becomes connected with the quadrate either by cartilage or by ligament.

The incus lies outside the vena capitis lateralis, the stapedial artery, and the hyomandibular branch of the facial, all of which pass between it and the auditory capsule, just as they pass between the quadrate and the capsule in reptiles and birds. A comparison of transverse sections of this region in these various groups brings out this remarkable uniformity (Pl. 12, figs. 18, 20; Pl. 13, figs. 29, 30). A manubrium develops from the malleus, extending downwards in the tympanum between the first gill-pouch and the ingrowing external auditory meatus (Pl. 12, figs. 16, 19). The chorda tympani, having passed round outside the laterohyal, runs forwards and inwards to the inner face of Meckel's cartilage, usually between the crus longus incudis and the manubrium. In Trichosurus its course seems to be more ventral than usual in mammals, as it runs well below the incus even in the new-born young (Pl. 12, fig. 19).

The development of the first gill-pouch is very similar to that described in Lacerta. In early stages it is continuous with the epiblast along an extensive region, but soon begins to separate off, and in 5 and 6 mm. Trichosurus embryos it is only connected with the epiblast dorsally at a point corresponding

to the closing slit in Lacerta (Pl. 12, fig. 14). Here arises the epiblastic proliferation which contributes to the geniculate ganglion, and marks the exact spot comparable in mammals, birds, and reptiles. The tympanic diverticulum grows out as usual from the more ventral and posterior region of the gill-pouch, while the dorsal apex, becoming quite detached, moves inwards, losing its connection both with the epiblast and with the ganglion. Subsequently various outgrowths of the wall of the tympanic cavity grow round the stapes and incus and malleus, leaving mesentery-like folds suspending these ossicles to the wall. The stapes may be said to push into the enlarging tympanic cavity from behind and above, while the incus and malleus push in from in front. The details of the development of the tympanic cavity have been described and illustrated very elaborately by Hammar (**18**) and Drüner (**10**), and need not detain us here. Gradually the mesoblastic tissue between the outgrowing tympanic diverticulum and the ingrowing external auditory meatus becomes thinned out, forming the tympanic membrane enclosing the manubrium of the malleus (Pl. 12, fig. 16).

The stapedial muscle can be seen extending back from the stapes to the skull-wall, below and on the inner side of the hyomandibular branch of the facial nerve (figs. 16, 23, and 25). Derived from the hyoid musculature this muscle is supplied by the seventh nerve (Killian (**24**)). On the contrary, the tensor tympani, derived from the pterygoid musculature of lower forms, is situated in front of the tympanic cavity, and is innervated from the fifth nerve. The tensor tympani of Mammalia stretches inwards from the malleus to the skull-wall; but the relation to the chorda tympani varies in different groups. For instance, the nerve passes above or dorsal to the tensor ligament in Man and Macacus; ventral or below the ligament in Sus, Canis, Arvicola, and Mus; while in Equus and Sciurus it passes through the ligament, according to the observations of Eschweiler (**14**) and Bondy (**3**). Doubtless the first position is the most primitive. It is that found in Trichosurus (fig. 17), and in

Mus (fig. 26), and corresponds to the relation of nerve and
muscle in reptiles.

Conclusion.—In the preceding pages it has been shown
that the chorda tympani in reptiles, birds, and mammals,
develops as a post-trematic branch of the facial nerve behind
the first gill-slit. As may be seen in the diagrams A, B, and
C (p. 144), owing to the outgrowth of the tympanic diverticu-
lum from the hinder region of the first gill-pouch, the chorda
comes to lie in front of this pouch when the slit closes and the
pouch separates off from the epidermis. The only known
exception to this rule is that of the gallinaceous birds, in
which the chorda is found to pass in front of the first gill-
pouch from its very first appearance. In the adult amniote
the chorda necessarily passes down anterior to the tympanum.
Although in certain forms like Sphenodon, where the mem-
brane is not very clearly delimited, the chorda may seem to
pass across the dorsal and anterior region of the tympanum,
the relative position of these parts remains essentially
unaltered.

It has also been shown how very constant throughout
ontogeny are the relations of the spiracular slit, vena capitis
lateralis, facial or stapedial artery, facial nerve, and chorda
tympani, in mammals, birds, and reptiles. Indeed, the early
stages of the lizard, duck, and Trichosurus, when the first
gill-pouch is still continuous with the epidermis, are so
similar that figures of any one of them would apply almost
equally well to the other two. Only unimportant differences
of relative size and proportion can be detected between them.
Later on divergencies occur owing to the great development
of the extra-columella in birds and reptiles, and to the
position taken up in mammals by the incus and malleus,
where they come to lie between the stapes and the tympanum ;
but even then the blood-vessels, muscles, nerves, and skeletal
parts retain their essential morphological relations. Only on
the supposition that the incus represents the quadrate, and
the malleus the articular, is this structure intelligible. As a
glance at diagrams D and E will show, the chorda tympani

really follows essentially the same course in reptiles and mammals. In both the hyoid arch, at its dorsal end, has two diverging branches: a stapedial fitting into the fenestra ovalis and an intercalary branch coming into contact with the skull. The hyomandibular branch of the facial nerve passes back over the stapes, and the chorda tympani runs from it outside the arch, then forwards between the spiracular

TEXT-FIG. 2.
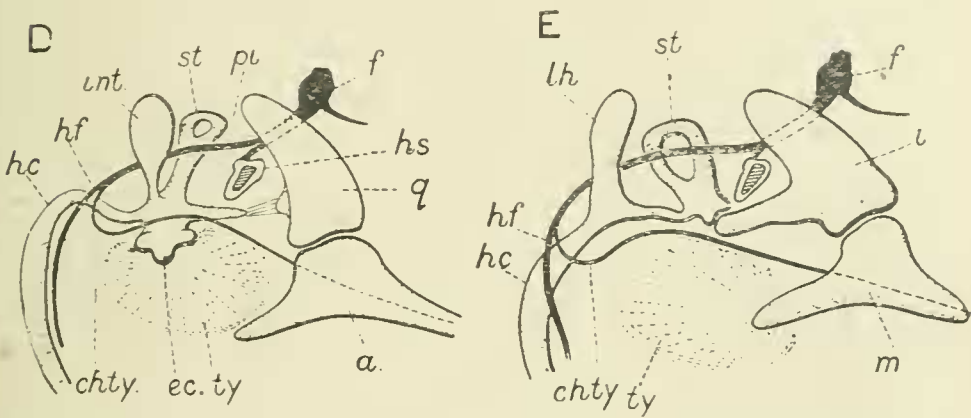
D and E. Diagrams showing the relation of the first and second visceral arches and the branches of the facial nerve to the closing first gill-slit and the developing tympanum in a reptile (D) and a mammal (E). *a*. Articular cartilage. *chty*. Chorda tympani. *ec*. Extra columella. *f*. Facial ganglion. *hc*. Hyoid cornu. *hf*. Hyomandibular branch of facial nerve. *hs*. Hyoid or spiracular gill-slit. *i*. Incus. *int*. Intercalary cartilage of processus dorsalis. *lh*. Intercalary or laterohyal cartilage. *m*. Malleus. *pi*. Processus internus. *q*. Quadrate. *st*. Stapes. *ty*. Tympanum. (Right-side view.)

opening (virtual in mammals) and the tympanum to the inner side of the articular or malleus. But, whereas in the reptile the columella has given rise to an extra-columella which grows into the tympanum below the chorda, in the mammal no such extra-columella is developed, and it is the malleus which comes into relation with the tympanum. Thus the relation of the chorda to the hyoid arch is really the same in the two cases. The articulation of the incus with the stapes is paralleled by the connection, cartilaginous or ligamentous, so frequently established between the columella and the

quadrate in reptiles and birds, and even in Amphibia. Whether the extra-columella be primitive among Reptilia is a doubtful point; but on the whole it seems probable that the Mammalia have lost it, on the gradual assumption of its functions by the incus and malleus. Accompanying this modification of the quadrate and articular to transmit vibrations from the tympanum, the jaws in mammals must, of course, have acquired a new mode of articulation. But this difficulty often urged against Reichert's theory may now be said to have disappeared owing chiefly to the discoveries of Seeley and Broom (5, 6). There is no need to go into this question in this paper. But it may be pointed out that these authors have shown that, in fossil Reptilia related to the ancestors of the Mammalia, the squamosal and dentary bones have gradually increased in importance, contributing more and more to the support of the lower jaw; while the quadrate and articular have dwindled in size, become loosened from the surrounding bones, and have, so to speak, been drawn into the service of the middle ear.

While the homology of these structures may now be considered as well established in the amniote vertebrates, their disposition in the Amphibia still presents serious difficulties. For in the only group which possesses a tympanum, the Anura, the ramus mandibularis internus (chorda tympani) is posterior to it. Drüner, indeed, concludes that the tympanum and tympanic cavity of the Amphibia and Amniota are not homologous (9). The evidence for such an extreme view seems quite insufficient, and Bender (2) has brought forward important facts with regard to the nerve-supply of the wall of the tympanitic cavity, which go far to prove that it is homologous throughout the terrestrial vertebrates and with the spiracular slit of fishes, a conclusion which is in agreement with the results of embryology. While accepting Bender's conclusion Gaupp still considers that the tympanum itself has become independently developed in Amphibia, reptiles, and mammals (17). But, while admitting that the position of the chorda is a serious difficulty in comparing the amphibian with the

reptilian structure, it would seem much more probable that there has been some relative shifting of parts.   Moreover, the presence of a characteristic notch behind the quadrate in fossil Stegocephalia indicates the possession of a tympanum, and those modern forms (Apoda and Urodela) which do not possess one have probably lost it, being secondarily adapted to a burrowing or aquatic mode of life.   The view of Gaupp that the tympanum of Reptilia is not homologous with that of Mammalia, chiefly because the former is situated above the Meckelian cartilage and the latter below it, seems to me greatly to exaggerate the importance of a comparatively trivial difference.   If the manubrium of the malleus represents the posterior process of the articular, the tympanum extends both above and below it, and the difference between the two types is small, and just such as we should expect to find accompanying the change of size and function of the incus and malleus.   Rather should we consider the modern reptilian and mammalian plan as showing two divergent types derived from some intermediate plan of structure perhaps to be discovered among the Theromorpha.

Summary.—A comparison of the development of the various structures of the middle-ear region in the lizard, duck, and mammal, shows a remarkable uniformity in their origin and relation.   The first gill-pouch separates off from the epidermis from below upwards ; at its dorsal edge is an epiblastic proliferation contributing to the geniculate ganglion. The tympanum is formed between the outer epidermis and an outgrowing diverticulum of the hinder lower region of the first gill-pouch.   The chorda tympani is a post-trematic branch of the facial nerve, developing behind the first or spiracular gill-slit, and passing down to the lower jaw between the tympanum and the closing spiracle.   The relation of these parts to the skeleton and blood-vessels is (with the exception mentioned below) constant throughout the Amniota, and is only intelligible on the view of Reichert that the proximal region of the columella corresponds to the stapes, the quadrate to the incus, and the articular to the malleus.

In the chick the chorda tympani develops as a pre-trematic branch of the facial nerve from its first appearance. In adult gallinaceous birds the chorda passes down directly from the geniculate ganglion in front of the tympanic cavity. This exceptional position is probably due to some secondary modification at present unexplained.

September 2nd, 1914.

LITERATURE.

1. Balfour, F. M.—' Comp. Embryology,' vol. ii, London, 1881.

2. Bender, O.—" Die Schleimhautnerven des Facialis," etc., ' Denkschr. d. Med.-nat. Ges. Jena,' Bd. vii, 1906.

3. Bondy, G.—" Beitr. z. vergl. Anat. d. Gehörorgane der Säuger." ' Anat. Hefte.' Bd. xxxv, 1907.

4. Broman, I.—" Die Entw. der Gehörknöchelchen beim Menschen." ' Anat. Hefte.' Bd. xi. 1899.

5. Broom, R.—" On the Structure of the Theriodont Mandible," etc.. ' Proc. Zool. Soc.,' London, vol. i. 1904.

6. ——— " On the Structure of the Skull in Cynodont Reptiles." ibid.. 1911.

7. Dixon, A. F.—" The Facial Nerve in Man." ' Journ. Anat. and Phys.,' vol. xxxiii. 1899.

8. Dreyfuss, R.—" Beitr. z. Entw. des Mittelohres u. d. Trommelfels," ' Morph. Arb.,' Bd. ii. 1893.

9. Drüner, L.—" Ueber d. Muskulatur d. Visceral-skelettes d. Urodelen." ' Anat. Anz.,' Bd. xxiii. 1903.

10. ——— " Ueber d. Anat. u. Entw. des Mittelohres b. Menschen u. b. d. Maus," ibid., bd. xxiv. 1904.

11. Cole, F. J.—" The Cranial Nerves and Lat. Sense Organs of Fishes," ' Trans. Linn. Soc.,' London, vol. vii, 1898.

12. Cords, El.—" Die Entw. d. Paukenhöhle von Lacerta agilis," ' Anat. Hefte.' Bd. xxxviii, 1909.

13. Emmel, V. E.—" The Relation of the Chorda Tympani to the Visceral Arches in Microtus," ' Journ. Compt. Neurol.,' vol. xiv, 1904.

14. Eschweiler, R.—" Z. vergl. Anat. d. Muskeln u. d. Topographie d. Mittelohres versch. Säugetiere," ' Arch. f. mik. Anat. u. Entw.,' Bd. liii, 1899,

15. Froriep, A.—" Anlagen von Sinnesorganen am Facialis," etc., ' Arch. Anat. u. Phys. Anat. Abt.' 1885.

16. Gaupp, E.—" Anat. Unters. ü. d. Nervensorgung d. Mund. u. Nasenhöhlendrüsen," ' Morph. Jahrb.,' Bd. xiv, 1888.

17. ———— " Die Reichertsche Theorie," ' Arch. Anat. u. Phys.,' Suppl., 1912.

18. Hammar, J. A.—" Die Entw. des Vorderdarms," etc., ' Arch. f. mik. Anat. u. Entw.,' Bd. lix, 1912.

19. Hasse, C.—" Z. Morph. d. Labyrinths der Vogel," ' Anat. Studien,' Bd. i. 1873.

20. Herrick, C. J.—" The Cranial and First Spinal Nerves of Menidia," ' Journ. Compt. Neurol.,' vol. ix, 1899.

21. Hoffmann. C. K.—" Reptilien," ' Bronn's Klassen. u. Ordnungen,' Bd. vi, 1891.

22. Jenkinson, J. W.—" Development of the Ear-bones in the Mouse," ' Journ. Anat. and Phys.,' vol. xlv, 1911.

23. Kastschenko, N.—" Das Schicksal d. embr. Schlundspalten bei Säugethiere," ' Arch. f. mik. Anat.,' vol. xxx, 1887.

23a. ———— " Das Schlundspaltsystem des Hühnchens," ' Arch. f. Anat. Anat. u. Phys., Anat. Abt.' 1887.

24. Killian. G.—' Z. vergl. Anat. u. vergl. Entw. der Ohrmuskeln." ' Anat. Anz.,' vol. v, 1890.

25. Kingsley, J. S., and Ruddick. W. H.—" The Ossicula Auditus and Mammalian Ancestry," ' Am. Naturalist,' vol. xxxiii. 1899.

26. Magnien, L.—" Recherches s. l'anat. comp. de la corde du tympan des Oiseaux," ' C. R. Ac. Sc.,' t. ci, 1885.

27. Neumayer, L.—Hertwig's ' Handb. d. vergl. Entw. d. Wirbeltiere,' Bd. ii. 1906.

28. Sheldon. R. E.—" The Phylogeny of the Facial Nerve and Chorda Tympani." ' Anat. Record,' vol. iii. 1909.

29. Smith, G. W.—" The Middle Ear and Columella of Birds," ' Quart. Journ. Micr. Sci.,' vol. 48, 1904.

30. Strong, O. S.—" The Cranial Nerves of Amphibia." ' Journ. Morph.,' vol. x, 1895.

31. Versluys. J.—' Entw. d. Columella auris b. d. Lacertiliern." ' Zool. Jahrb.. Abt. Anat. u. Ont.,' vol. xix. 1903.

EXPLANATION OF PLATES 11, 12, AND 13,

Illustrating Mr. Edwin S. Goodrich's paper on "The Chorda
Tympani and Middle Ear in Reptiles, Birds, and
Mammals."

LETTERING OF PLATES.

a. a. Aortic arch. *a. c.* Auditory capsule. *a. i. r.* Anterior inner
recess of tympanic cavity. *a. o. r.* Anterior outer recess. *art.* Arti-
cular cartilage. *a. s.* Auditory sac. *b.* Blastema extending from
stapes to hyoid. *bo.* Epiblastic proliferation or branchial "sense organ"
of facial nerve. *bra.* Branchial arch. *bs* 1–4. First to fourth branchial
slits. *c.* Small cartilage of hyoid arch, = epihyal? *car.* Internal
carotid artery. *col.* Columella auris. *eam.* Invagination to form ex-
ternal auditory meatus and external wall of tympanum. *ep.* Epiptery-
goid. *et.* Eustachian tube. *f.* Facial ganglion and nerve. *fb.* Fore-
brain. *gl.* Glosso-pharyngeal ganglion and nerve. *h.* Hyoid bar. *ha.*
Blastema of hyoid arch. *hart.* Hyoid arterial arch. *hb.* Hindbrain.
hc. Hyoid cornu. *hf.* Hyomandibular branch of facial nerve. *hs.*
Hyoid or spiracular slit. *hsp.* Pouch of hyoid slit. *intc.* Intercalary
cartilage from dorsal process. *lsk.* Lateral cranial wall. *man.* Manu-
brium mallei. *md.* Mandibular bar. *mda.* Blastema of mandibular
arch. *mk.* Meckel's cartilage. *ms.* Extra-columellar muscle. *oc.* Occi-
pital cartilage. *os.* Optic stalk. *par.* Paroccipital process. *pb.* Pro-
cessus brevis incudis. *pl.* Processus longus incudis. *ppart.* Posterior
process of articular cartilage. *pr.* Posterior recess of tympanic cavity.
prant. Anterior process of columella. *prp.* Posterior process of extra-
columella. *psk.* Process of skull. *quad.* Quadrate cartilage. *sta.*
Stapedial artery or facial artery. *sth.* Stylohyal cartilage. *stm.* Sta-
pedial muscle. *tr.* Trigeminal nerve and ganglion. *tt.* Tensor tym-
pani muscle. *tyd.* Tympanic diverticulum. *v.* Vagus ganglion and
nerve. *vcl.* Vena capitis lateralis.

[In the reconstructions here figured the nerves are in black; the
pharynx, gill-pouches, and tympanic cavity in green; the veins in
blue; the arteries in red; the cartilage in purple. In the earliest stages
the blastema representing the skeleton is indicated by purple dots.]

PLATE 11.

Fig. 1.—Reconstruction of a portion of the right side of the head of
a Lacerta embryo at an early stage when the first or spiracular slit is
still widely open to the exterior. The nerves and gill-slits are recon-
structed on the outline of a section near the middle line.

Fig. 2.—The same with the blood-vessels added.

Fig. 3.—Similar view of a later stage of Lacerta, when the first gill-slit is partially closed, and the blastemata of the mandibular and hyoid arches are visible.

Fig. 4.—Similar view of a corresponding stage of an embryo duck (four and a half days). In this, in fig. 5, and in some of the following figures, the epidermis indicating the surface of the embryo has been shown.

Fig. 5.—Reconstruction of a portion of the right side of an embryo Trichosurus vulpecula 5 mm. long (I, A, '01). The endodermal pouch of the first slit is still continuous with the epidermis at a point not represented in the figure, the surface of the head having been cut away.

Fig. 6.—Reconstruction of the right side of a thick horizontal section of the head of Lacerta at a stage when the hyoid arch is still continuous with the columella by means of procartilage. View from above (dorsal) the vena capitis lateralis having been removed. The first gill-pouch has separated from the epidermis.

Fig. 7.—Right side of the head of an older Lacerta embryo. Only the skeletal and nervous systems have been reconstructed, but the pharynx and blood-vessels are shown as cut in the section nearest the median line. For the sake of clearness the distal region of the columella has been cut away.

Fig. 8.—More complete reconstruction of a portion of the same specimen as shown in fig. 7, with the complete columella, the arteries and the gill-pouch. A narrow strip of vaguely defined tissue still connects the top of the hyoid cornu with the extra-columella.

Figs. 9, 10, 11.—Reconstructions of the quadrate region of a late Lacerta embryo seen from behind (posterior view). In figs. 10 and 11 only the skeleton and tympanic cavity are shown, the columella being completed in both. Fig. 11 fits on to fig. 10, and shows the posterior upper part of the quadrate and the tympanic recesses. Fig. 9 resembles fig. 10, but has the nerves, tympanic cavity, and arteries included. The position of the vena capitis lateralis is indicated by a dotted ring.

Fig. 12.—Reconstruction of the right auditory region of a five-day chick embryo. The first gill-pouch is still continuous with the epiblast, and the chorda tympani runs down anterior to it. The skeleton is present only as a vaguely defined blastema at this stage.

PLATE 12.

Fig. 13.—The right auditory region of an eight-day chick embryo. In the thick slice reconstructed only the inner region of the ingrowing external auditory meatus appears. The upper posterior region of the quadrate has been cut away to expose the underlying structures.

Fig. 14.—Reconstruction of a portion of the right side of the head of an embryo of Trichosurus vulpecula 7·25 mm. long (XII, A, '01). The first gill-pouch has just separated from the epiblast at a point below the " branchial sense organ " *bo.*

Fig. 15.—Dorsal view of a reconstruction from transverse sections of the right side of the head of an embryo Trichosurus vulpecula 6 mm. long. The first gill-pouch is still continuous with the epiblast, and the chorda tympani passes behind and below it. The thick slice does not include the whole vena capitis lateralis, and only the most ventral part of the auditory sac lying above the other structures.

Figs. 16 and 17.—Reconstructions of the right auditory regions of the head of an embryo Trichosurus vulpecula 17 mm. long. To expose the stapes and other structures the incus and malleus have not been included in fig. 17.

Figs. 18, 19, 20.—Reconstruction of three consecutive thick transverse slices through the left auditory region of the head of a newborn Trichosurus vulpecula. The reconstructions are seen from in front (anterior view), and the hind surface of the slices 18 and 19 fit on to the front surface of the slices 19 and 20 respectively.

Fig. 21.—Ventral view of a thick slice of the right auditory region of the head of an embryo of Trichosurus vulpecula 9·5 mm. long, reconstructed from transverse sections. The skeleton is procartilagenous. The stapes is seen through the first gill-pouch, and is continuous with the procartilage of the hyoid arch.

Fig. 22.—Similar view, but from the dorsal surface, of the left auditory region of an embryo mouse at a slightly later stage.

PLATE 13.

Figs. 23 and 24.—Similar dorsal views of the same region of a fourteen-day embryo mouse. A portion of the skull has been cut away to expose the stapedial muscle in fig. 23. In fig. 24 the skeleton of the visceral arches and the blood-vessels are shown.

Figs. 25 and 26.—Two consecutive thick slices of the right auditory region of an older embryo mouse 22 mm. long, viewed from the dorsal surface and reconstructed from transverse sections.

Fig. 27.—Longitudinal sagittal section through the middle-ear region of the Lacerta embryo drawn in fig. 3. *Cam.*

Fig. 28.—Similar section of the embryo duck drawn in fig. 4. *Cam.*

Figs. 29 and 30.—Transverse sections of the ear region of the Lacerta embryo shown in fig. 9. Fig. 29 represents a section in front of the columella, and fig. 30 through the columella. *Cam.*